

Good-genes effects in sexual selection

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The magnitude of the effect of good genes as a viability benefit accruing to choosy females remains a controversial theoretical and empirical issue. We collected all available data from the literature to estimate the magnitude of good-genes viability effects, while adjusting for sample size. The average correlation coefficient between male traits and offspring survival in 22 studies was 0.122, which differed highly significantly from zero. This implies that male characters chosen by females reveal on average 1.5% of the variance in viability. The studies demonstrated considerable heterogeneity in effect size; some of this heterogeneity could be accounted for by differences among taxa (birds demonstrating stronger effects), and by differences in the degree of mating skew in the species (high skew reflecting stronger effects). Although these results suggest that viability-based sexual selection is widespread across taxa, they indicate that the effect is relatively minor. Finally, there was also an effect of publication year in that the more recent studies reported reduced effects. This may reflect publication biases during paradigm shifts of this debated issue, but it should also be recalled that the studies have only partly estimated the full fitness consequences of mate choice for offspring.

Keywords: experiment; mate preference; meta-analysis; secondary sexual character; viability

1. INTRODUCTION

Sexual selection has attracted considerable attention from evolutionary biologists during recent years because the functional significance of strong female preferences for exaggerated male secondary sexual characters remains an enigma (see, for example, Andersson 1994). Although it has been readily accepted that females may choose mates based on direct fitness benefits, for example caused by male parental care, there is little agreement about the magnitude of indirect fitness benefits in terms of genetically based male attractiveness or viability. Furthermore, the particularly intense theoretical debate over the possibility of good-gene effects may have generated biases in publication of results (Alatalo *et al.* 1997). The risk of publication bias is particularly likely here, because the expected effect size can be very small, as suggested by the general view that the heritability of fitness certainly does not exceed 0.10 (see Gustafsson 1986; Charlesworth 1987; review in Burt 1995).

A major problem with viability effects of sexual selection, so-called good-genes sexual selection, is that persistent directional selection caused by directional female mate preferences is expected to deplete any genetic variation in viability because alleles coding for the preferred traits go to fixation (review in Andersson 1994). Several mechanisms have been proposed to maintain additive genetic variation in viability (Hamilton & Zuk 1982; Pomiankowski *et al.* 1991; Iwasa *et al.* 1991; review in Roff 1997). This argument about sexual selection depleting genetic variance has been addressed by

reviews of empirical studies demonstrating considerable additive genetic variation in male secondary sexual characters (Pomiankowski & Møller 1995), female mate preferences (Bakker & Pomiankowski 1995) and fitness (Burt 1995).

Although viability effects of sexual selection have been suggested to be small at best when the genetic variation is maintained by the frequency of deleterious mutations (Kirkpatrick 1996), this remains a hypothetical issue that awaits careful empirical assessment. A recent comparative study has demonstrated that bird species with intense sexual selection, as caused by extra-pair paternity, tend to have significantly more (not less) genetic variability, measured from allozymes and RAPDs, than species with little or no extra-pair paternity (Petricie *et al.* 1998). This result could be due to intense sexual selection mainly being present in species with high genetic variability, or to sexual selection promoting genetic variability (Petricie *et al.* 1998).

The aims of the present study were to quantify the viability effects of sexual selection. This was carried out based on a literature survey of studies of good-genes sexual selection. Although good-genes effects may be expressed as enhanced growth, fecundity or survival, we have concentrated our efforts on reviewing the literature on survivorship effects because most studies have addressed this major fitness component, and because lifetime reproductive success in a diverse array of organisms depends more on longevity than on any other life-history trait (Clutton-Brock 1988; Newton 1989). For completeness we also provide a list of additional studies with other viability effects. The assessment of the magnitude of viability effects was done by using meta-analysis as a stringent

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way of summarizing a body of literature while taking sampling effort and potentially confounding variables into account (Hedges & Olkin 1985; Rosenthal 1991, 1994). Meta-analysis also has the advantage of being able to resolve the problem of type II statistical errors, which are likely to be common in areas of research where large data sets are difficult to obtain and the power of statistical tests is therefore low.

2. MATERIALS AND METHODS

Data on viability effects of sexual selection were obtained by an extensive search of the literature and by correspondence with researchers in the field. We contacted more than 25 scientists with a long-standing interest in sexual selection and asked for additional information on unpublished studies investigating viability effects. This resulted in a total of 22 studies for which there was information on survival of offspring.

Meta-analyses are problematic if null results tend not to be published (Hunter & Schmidt 1990). Obviously, we can never know how many unpublished studies of negative results are available, but this problem can be addressed by calculating the failsafe number of publications, which is the number of null results needed to nullify an overall effect (Rosenthal 1991, p. 104).

Studies of viability effects in sexual selection have always been controversial, but there is still some reason to believe that studies with positive results are more likely to have been published. However, we are unaware of any unpublished studies of viability effects in sexual selection based on our own experience. Similarly, we are unaware of the presence of such studies despite having asked more than 25 colleagues who have been working in this field for a very long time.

We used Pearson's product-moment correlation coefficient as a measure of effect size; this coefficient has the intuitive appeal that the square of its value represents the amount of variance accounted for by a particular relation, and it also corresponds to the correlated response to selection in quantitative genetics. We searched the literature for correlation coefficients, or other statistics that could be converted into correlation coefficients, based on the relation between offspring survival and male characters.

The variables of interest were classified in the following ways: (i) whether the target of selection had been identified based on observations or experiments, or whether that was not the case; (ii) the magnitude of the viability effect, calculated as the correlation coefficient between a secondary sexual character and viability of the offspring; (iii) the female mate preference for the male trait estimated from observational or experimental studies, expressed as the correlation coefficient between the male character and male mating success; (iv) the phenotypic coefficient of variation of the male trait obtained from the source publications or from personal communication with the scientists in question (to make these coefficients comparable, we transformed coefficients of variation for volumes or masses by means of a cube-root transformation); (v) whether the study in question was based on an experimental approach by allocating females to males, or based on observations; (vi) the mating skew of the species, ranked as either 1, 2 or 3, where species with little variance in male success (such as socially monogamous species) were ranked as 1, species with large variance in male success (such as lekking species) were ranked as 3, and the remaining species were ranked at an intermediate level. Independent ranks

by the authors were strongly positively correlated (Kendall rank-order correlation coefficient, $\tau=0.90$, $n=22$, $p<0.001$). The entire data set is reported in Appendix A.

If there is statistically significant heterogeneity in effect size among studies, this implies that one or more moderator variables may influence the relation between the variable of interest and phenotypic or ecological variables. The absence of significant heterogeneity implies that we have no formal statistical justification for expecting such an effect in the data available, although additional confounding variables may have been missed. Given statistically significant heterogeneity among effect sizes in the meta-analysis (see below for methods), we tested for the influence of five moderator variables that we believed could potentially explain some of this heterogeneity in the different tests: (i) whether the viability effect was larger in birds than in other groups of organisms (among the published studies, there is an apparently greater effect of good-genes sexual selection in birds than in many other organisms (Alatalo *et al.* 1998)); (ii) whether the viability effect is greater when the target of sexual selection has been identified (effects are often assumed to be weaker if the viability effect cannot be readily related to the variable of interest); (iii) whether the effect size was related to the intensity of the mate preference (females have been suggested to demonstrate stronger mate preferences, if there is more to gain in terms of fitness benefits (Petrie & Lipsitch 1994)); (iv) whether the viability effect is related to the phenotypic coefficient of variation of the male trait, because it is likely that females are better able to discriminate when a character is particularly variable (Searcy 1979); (v) whether the viability effect is stronger in experimental than in observational studies, because experiments are likely to remove effects of potentially confounding variables; (vi) whether the viability effect is related to mating skew, which may reflect the intensity of sexual selection.

(a) *Meta-analysis*

The measure of effect size used was Pearson's correlation coefficient. If the original sources did not provide a correlation coefficient, we transformed the statistics into a correlation coefficient by using the formulae for transformation given by Rosenthal (1994, table 16.1). In cases where only probabilities were reported, these were transformed into Pearson correlation coefficients by means of the standard transformation (Sokal & Rohlf 1995). When non-parametric tests were reported (only two cases), calculated effect sizes were based on the reported values of p . Pearson correlation coefficients were subsequently transformed by means of Fisher's transformation to z -values, on which all subsequent analyses were performed. This measure of effect size was adjusted for sample size using $n-3$ as an adjustment factor (Rosenthal 1991, pp. 27–28), based on the assumption that a larger sample size should provide a more reliable estimate of the unknown, true relation.

We tested for an overall effect with the effect size adjusted for sample size after z -transformation to test whether it differed significantly from zero (Rosenthal 1991), using the equation:

$$\text{mean weighted } z_r = \sum (n_j - 3) z_{rj} / \sum (n_j - 3),$$

where z_{rj} is the z -transformed effect size for analysis unit j . The mean weighted z_r -values were tested against the null hypothesis of no effect by examining the significance of their associated r -values.

An estimate of heterogeneity in effect sizes among samples was subsequently calculated by using the formula provided by Rosenthal (1991, pp. 73–74):

$$\chi^2 = \sum (n_j - 3)(z_{ij} - \text{mean } z_r)^2,$$

which has a χ^2 distribution with $K-1$ degrees of freedom, where K is the number of analysis units.

Provided that there was statistically significant heterogeneity among effect sizes of studies, we proceeded by testing for the effects of potential explanatory variables by calculating a standard normal deviate, as suggested by Rosenthal (1991, pp. 79–84):

$$\sum \lambda_j z_r / \left(\sqrt{\sum (\lambda_j^2 / w_j)} \right),$$

where λ_j is the contrast weight determined by a hypothesis of the analysis unit (samples, species), chosen so that the sum of values of j equals zero. The weighting factor is $1/n_j$, where n_j is the number of samples in each of the j categories. For example, a contrast based on whether a trait has been identified as the target of sexual selection would be $\lambda_1 = -n_1$, where n_1 is the number of studies with the trait identified, and $\lambda_2 = n_2$, where n_2 is the number of studies with the trait remaining unidentified. w_j is the inverse of the variance of the effect size for the analysis unit. The 95% confidence intervals were calculated according to Hedges & Olkin (1985, pp. 230–232).

The failsafe number of studies, X , needed to nullify an effect was calculated, following Rosenthal (1991, p. 104) as:

$$X = \left(\sum z_j \right)^2 / 2.706 - K,$$

where $z_j = z_{ij} \sqrt{(n_j - 3)}$ and K is the number of analysis units.

We conducted multivariate analyses to determine the independent effects of different moderator variables, using \log_{10} -transformed effect size as an additional independent variable.

3. RESULTS

The unweighted average effect size for viability was $z=0.221$; this value is equivalent to $r=0.218$ (95% CI=0.181, 0.255, $n=22$). This differs significantly from no effect ($t=12.01$, $p<0.001$). The sample-size weighted average effect had an r -value of 0.122 (95% CI=0.085, 0.159, $n=22$); this also differs significantly from no effect ($t=6.61$, $p<0.001$). The failsafe number, which refers to the number of unknown additional studies that would be needed to eliminate an overall effect's significance at the 5% level when those studies showed an average null result (mean $z=0.00$), was 387. There was statistically significant heterogeneity among studies ($\chi^2=197.52$, d.f.=21, $p<0.001$). Hence it was justified to attempt to determine explanatory variables that could account for some or all of this heterogeneity.

First, we separated out the studies of birds and pooled the remaining studies because bird studies have been assumed to have larger effects than others. However, we found no evidence of such an effect in a contrast test ($z=-0.491$, $p=0.62$; figure 1). Second, we found a significant difference between studies in which a specific trait had been identified as the target of selection and those in which that was not the case ($z=6.545$, $p<0.0001$; trait not identified: $z=0.042$ (95% CI = -0.089, 0.173), $n=3$; trait

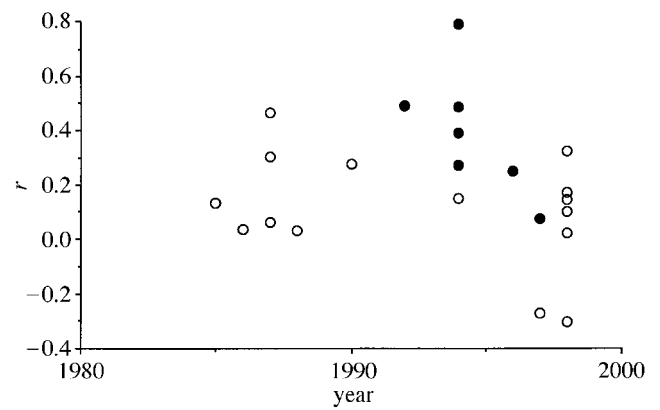


Figure 1. Untransformed effect sizes (Pearson product-moment correlation coefficients) in relation to year of publication of different studies of viability effects and taxa. Filled circles, birds; open circles, other taxa.

identified: $z=0.129$ (95% CI=0.091, 0.167), $n=19$). Studies in which the target of selection remains unidentified will obviously display low effect sizes because we are not contrasting categories of males that necessarily differ in phenotypic traits preferred by females. Third, we found no significant difference when comparing studies based on observational and experimental approaches ($z=1.853$, $p=0.064$). Fourth, we did not find any evidence of species with the three categories of mating skew differing significantly in effect size ($z=0.459$, $p=0.64$).

We determined whether the continuous variables for mate preference (Fisher's z -transformed correlation) and phenotypic coefficient of variation (\log_{10} -transformed; dependent variables) were related to the magnitude of the viability effect, while controlling statistically for any effects of sampling effort by using the \log_{10} -transformed sample size as an additional independent variable (the two independent variables were thus effect size for viability and sample size). For mate preference, the multiple regression model was not significant ($F=0.34$, d.f.=2,15, $r^2=0.04$, $p=0.72$), and the partial regression coefficient for the mate preference was far from significant ($b(\text{s.e.})=0.23$ (0.43), $p=0.59$). The multiple regression model for the phenotypic coefficient of variation for the male trait was not statistically significant ($F=2.82$, d.f.=2,13, $r^2=0.30$, $p=0.10$), and the partial regression coefficient for mate preference was not significant ($b(\text{s.e.})=0.245$ (0.193), $p=0.23$).

Because these different variables may not be statistically independent, we performed a multivariate analysis with the z -transformed correlation coefficient as the dependent variable and all the variables listed above as independent variables. The simplest model that accounted for the variance in the data included taxon, mating skew and year of publication as independent variables. This analysis showed that there were strong independent effects of taxon, mating skew and year of publication on effect size (table 1). Studies of birds had relatively high effect sizes and so did the studies involving species with high mating skew. Finally, the more recent studies illustrated reduced effect sizes (figure 1).

Table 1. *Multiple regression analysis of effect size (viability as the dependent variable) in relation to taxon (dummy variable), mating skew (dummy variable) and year of publication (independent variables)*

(Regression model: $F=17.72$, d.f. = 3, 18, $r^2=0.75$, $p<0.0001$.)

independent variable	<i>b</i> (s.e.)	<i>p</i>
taxon	0.708 (0.099)	<0.0001
mating skew	0.309 (0.060)	<0.0001
year of publication	-0.026 (0.008)	0.0035

4. DISCUSSION

The analysis of viability effects arising from sexual selection demonstrated an average unweighted effect of 0.22 across a total of 22 studies of a range of different taxa. Weighting by sample size reduced the effect to 0.12; this result implies that male secondary sexual characters explain on average 1.5% of the variance in offspring survivorship, an effect comparable to the estimates of heritability of fitness (see Gustafsson 1986; Charlesworth 1987; Burt 1995). However, this small effect may have considerable consequences on an evolutionary time-scale. The failsafe number of studies was 387, more than ten times the number of studies included and well above the recommended number for a robust result (Hedges & Olkin 1985; Rosenthal 1991, 1994). Maternal and common environment effects may have inflated the effect in some studies, where this factor could not be controlled experimentally. Even in experiments where females were assigned randomly to mates (see, for example, Petrie 1994), or in studies where potential maternal effects were investigated statistically (see, for example, Hasselquist *et al.* 1996), it is still possible that maternal effects may have affected the outcome through differential parental investment. However, negative relations between male ornamentation and male parental care in other species (such relations are common in species with male parental care and intense sexual selection (Møller & Thornhill 1998)) may have reduced rather than increased the probability of offspring survival.

The second finding of our study was the considerable amount of heterogeneity in effects among studies. What accounts for this variation in effect size among studies? We investigated a number of factors that we presumed might affect the magnitude of any good genes. We found that effects were in general stronger for studies where the target of selection had been identified than for those with an unknown target of selection. There were no significant effects of the dichotomy of experimental versus observational studies and studies of birds versus other taxa.

In the multivariate analysis, there was a clear significant effect for mating skew, taxon and year. None of the other moderator variables reached statistical significance in the multivariate test. The effect of mating skew was not clear-cut: mean weighted r for high skew = 0.19, $n=8$, mean weighted r for intermediate skew = 0.07, $n=9$ and mean weighted r for low skew = 0.12, $n=5$. The lack of effect for the univariate analysis probably arose as a consequence of correlations between moderator variables.

The effect of taxon reached significance in the multivariate analysis, although the effect may be real or just reflect the particular choice of species included in the present analysis.

The effect of publication year is somewhat surprising, because effect size was relatively large before 1995 (weighted $r=0.20$, $n=13$), whereas mean effect in later studies was non-significant and close to zero (weighted $r=0.08$, $n=8$). This finding may resemble that proposed by Alatalo *et al.* (1997), who suggested that paradigm shifts caused publication bias after the good-genes idea became generally accepted. However, whereas Alatalo *et al.* (1997) reported an increase in such effects with year of publication, the present study found exactly the opposite effect. The temporal change of events may be what one should expect at the present stage of a possible paradigm shift after the early enthusiasm for good-genes effects. Of course, numerous factors may change with time, and it is thus not easy to pinpoint any particular factor as being responsible for such changes. Given the very small sample sizes used in the present study, such differences may even be random effects due to the particular kinds of studies being published in any particular year.

Many studies of good-genes sexual selection are based on laboratory data, and this feature may render absent some viability effects that otherwise occur in the wild. If natural causes of death are partly or completely eliminated in a laboratory environments, correlations between viability and the expression of secondary sexual characters may disappear or even change sign. For example, predation is likely to have been eliminated from all laboratory studies of sexual selection, whereas some effects of diseases and parasites may still be present even under laboratory conditions. A planned contrast test between laboratory and field studies revealed no statistically significant difference between the two categories.

Trade-offs between viability and other components of fitness are central to life-history theory (Roff 1992; Stearns 1992). We have only analysed the survival effect of good-genes sexual selection; other effects, such as growth performance, developmental time and fecundity, could not be analysed because there were fewer data available. This could cause bias in the conclusions because particular taxa lend themselves more readily to studies of survivorship effects. Not surprisingly, 7 of the 22 studies with survival effects were based on birds as study organisms; none of the remaining 11 studies of other viability effects was based on birds. Although this difference is not statistically significant (Fisher exact probability test: $p=0.0674$), this observation indicates a bias of survivorship studies towards certain groups of vertebrates. The emphasis on viability may also explain the surprising results of females significantly choosing males with low viability, leading to a negative correlation between viability and the expression of secondary sexual characters in some studies (see, for example, Whittier & Kaneshiro 1995; Horne 1998). Such negative fitness effects of mate choice should be eliminated by selection unless counterbalanced by other fitness benefits of mate choice. A number of other studies have shown positive correlations between various fitness components and the expression of secondary sexual characters (see, for example,

Møller 1994; Petrie 1994; Hasselquist *et al.* 1996; Welch *et al.* 1998).

In conclusion, we have found a small correlation coefficient between offspring survival and the expression of male secondary sexual characters across a relatively large number of organisms. This finding is in accordance with the hypothesis that females may obtain genetically based viability benefits from their mate choice.

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APPENDIX A

Table A1. *Sexual selection studies of viability effects*

(Information on secondary sexual trait being identified, sample size, effect size (Pearson product-moment correlation coefficient), female mate preference (Pearson product-moment correlation coefficient between expression of male trait and male mating success), phenotypic coefficient of variation, whether the study was observational (1) or experimental (2), mating skew ranging from low (1) through intermediate (2) to high (3), and reference.)

species	trait identified	n	effect	preference	CoV	mating experiment	skew	reference
studies with estimates of survival effects								
<i>Acrocephalus arundinaceus</i>	yes	77	0.250	0.936 ^a	12.600	1	1	Hasselquist <i>et al.</i> (1996)
<i>Bufo americanus</i>	yes	48	0.147	0.677	1.147	2	3	Howard <i>et al.</i> (1994)
<i>Bufo woodhousei</i>	yes	42	0.279 ^b	—	—	2	3	Mitchell (1990)
<i>Clethrionomys glareolus</i>	yes	46	−0.304	0.801	34.952	2	2	Horne (1998)
<i>Coelopa frigida</i>	yes	136	0.301	0.137	10.800	2	2	Crocker & Day (1987)
<i>Drosophila montana</i>	yes	100	0.173	0.287	9.680	2	2	Hoikkala <i>et al.</i> (1998)
<i>Ficedula albicollis</i>	yes	1174	0.075	0.523	20.050	1	1	Gustafsson <i>et al.</i> (1995)
<i>Galerucella nymphaeae</i>	yes	35	−0.272	0.475	3.681	2	2	Parri <i>et al.</i> (1998)
<i>Gryllus bimaculatus</i>	yes	378	0.061	0.634	21.400 ^c	2	2	Simmons (1987)
<i>Hirundo rustica</i>	yes	36	0.487	0.380	11.860	1	1	Møller (1994)
<i>Hygrolycosa rubrofasciata</i>	yes	71	0.143	0.366	88.100	2	3	Alatalo <i>et al.</i> (1998)
<i>Hyla crucifer</i>	no	24	0.030	0.101	4.500	2	2	Woodward <i>et al.</i> (1988)
<i>Hyla versicolor</i>	yes	179	0.323	0.924 ^d	20.94	2	3	Welch <i>et al.</i> (1998)
<i>Lutzomyia longipalpis</i>	no	173	0.020	0.280	—	2	3	Jones <i>et al.</i> (1998)
<i>Parus caeruleus</i>	yes	91	0.272	0.639	20.754	1	1	Kempnaers <i>et al.</i> (1992)
<i>Parus major</i>	yes	36	0.493	—	9.900	2	1	Norris (1993)
<i>Pavo cristatus</i>	yes	8	0.790	0.587	6.400	2	3	Petrie (1994)
<i>Phasianus colchicus</i>	yes	23	0.390	0.513	14.328	1	2	von Schantz <i>et al.</i> (1994)
<i>Scaphiopus couchi</i>	yes	36	0.464	—	—	2	3	Woodward (1987)
<i>Scaphiopus multiplicatus</i>	yes	12	0.036	—	—	2	2	Woodward (1986)
<i>Sepsis cynipsea</i>	yes	75	0.100	0.195	142.170	2	3	Blanckenhorn <i>et al.</i> (1998)
<i>Tribolium castaneum</i>	no	46	0.133	0.190	—	2	2	Boake (1985)
studies with other estimates of viability ^c								
<i>Achroia grisella</i>	yes	—	—	—	—	—	—	Jia & Greenfield (1997)
<i>Bufo bufo</i>	yes	24	—	0.425	2.747	2	3	Semlitsch (1994)
<i>Ceratitis capitata</i>	yes	86	−0.318	—	—	2	3	Whittier & Kaneshiro (1995)
<i>Cyrtodiopsis dalmanni</i>	yes	—	—	—	—	—	—	Wilkinson <i>et al.</i> (1998)
<i>Drosophila melanogaster</i>	no	136	0.365	—	—	2	3	Partridge (1980)
<i>Drosophila melanogaster</i>	no	—	—	—	—	—	—	Schaeffer <i>et al.</i> (1984)
<i>Drosophila melanogaster</i>	no	155	0.920	—	—	1	3	Taylor <i>et al.</i> (1987)
<i>Gryllus bimaculatus</i>	yes	—	—	—	—	—	—	Wedell & Tregenza (1999)
<i>Nauphoeta cinerea</i>	yes	164	0.184	0.200	—	1	2	Moore (1994)
<i>Poecilia reticulata</i>	yes	96	—	—	—	2	2	Nicoletto (1995)
<i>Poecilia reticulata</i>	yes	34	0.650	0.735	4.300	2	2	Reynolds & Gross (1992)

^a Catchpole *et al.* (1986).

^b Based on the contrast in table 4 in Mitchell (1990) and R. Thornhill (personal communication).

^c L. Simmons (personal communication).

^d Klump & Gerhardt (1987).

^e These studies are only listed as references that have been checked for survival effects of sexual selection.

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